

Competition between simultaneous stimuli modulated by location probability in hemispatial neglect

Joy J. Geng^{a,*}, Marlene Behrmann^b

^a *Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK*

^b *Department of Psychology, Carnegie Mellon University, Pittsburgh, USA*

Received 15 June 2005; received in revised form 21 September 2005; accepted 30 October 2005

Available online 5 December 2005

Abstract

Many aspects of spatial neglect can be explained as arising from competition for attentional selection, with salient ipsilesional stimuli emerging as the winner more often than contralesional stimuli. The outcome of the competition, however, can be affected both by bottom-up perceptual factors such as the gestalt properties of the display and by top-down factors such as expectancy or stimulus blocking. This study examines whether the competition for attentional selection can be modulated by manipulating the probability of the target's location in hemispatial neglect. Five patients with left-sided hemispatial neglect and a group of control participants performed a visual target discrimination task. In equal probability blocks, the target appeared randomly in any of six possible horizontal locations (three left, three right) whereas in biased blocks, the target appeared in the mid-location on the left on 50% of the trials and in each of the other locations on 10% of the trials. The target appeared either alone or was accompanied by a distractor on the opposite side. The results showed that the spatial bias facilitated detection of all left-sided targets in the neglect group, but was more spatially specific in the control group. Furthermore, while distractors on either side interfered with target processing in both groups, the patterns differed across the visual field. Finally, the magnitude of facilitation due to the bias was greatest in the condition with the most inhibition, i.e. a left-sided target accompanied by a right-sided distractor in the neglect group. These data underscore the competitive push–pull relationship between different bottom-up and top-down attentional factors, particularly within neglect patients, in whom a strong ipsilesional attentional bias already exists.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Hemispatial neglect; Extinction; Top-down; Spatial processing; Selective attention; Visual perception

1. Introduction

Many recent theories have conceptualized neglect as resulting from a competitive imbalance between sensory inputs from the left and right sides of space. Following damage to the right hemisphere of the brain, there is a bias such that information presented to the contralesional left side loses out in the competition for attentional selection against objects presented on the ipsilesional right (Driver, 1998; Duncan, Humphreys, & Ward, 1997; Kinsbourne, 1993). The idea that ipsilesional and contralesional stimuli compete for attentional selection has a relatively long history in the field of neglect with the early reports that contralesional neglect is exacerbated when there is a simultaneous stimulus on the ipsilesional side (Bender, 1952; Critchley, 1953). That contralesional stimuli can

be reported under some conditions has been taken as evidence against a strictly sensory deficit being responsible for neglect and in favor of a more attentional explanation.

The view of neglect as resulting from a competitive imbalance is compatible with the view of attention in the normal, healthy brain in which there is a fundamental neural limitation with the result that stimuli compete for selection and representation (Desimone, 1999; Desimone & Duncan, 1995b; Duncan, 1984; Mattingley, 2002). Recent support for this dynamic competitive account of neglect has come from many observations that the disregard of contralesional stimuli is not absolute; rather, when cued by perceptual factors or instructed to attend to the left (and also when instructed to ignore the right), neglect patients may succeed in processing the contralesional information as a result of boosting the strength and salience of this information (Karnath, 1988; Posner, Walker, Friedrich, & Rafal, 1984; Riddoch & Humphreys, 1983). For example, a contralesional stimulus is detected better when it is perceptually similar to the ipsilesional stimulus (for example, two brackets) than when it is perceptually

* Corresponding author. Tel.: +44 20 7679 1123; fax: +44 20 7813 2835.
E-mail address: j.geng@ucl.ac.uk (J.J. Geng).

dissimilar (for example, a bracket and a dot) (Ward, Goodrich, & Driver, 1994; see also Baylis, Driver, & Rafal, 1993; Danckert, Maruff, Kinsella, de Graaff, & Currie, 1999; Ptak, Valenza, & Schneider, 2002). Additionally, the extent to which the bilateral stimuli are connected (Driver, Mattingley, Rorden, & Davis, 1997), show polarity (Gilchrist, Humphreys, & Riddoch, 1996), collinearity (Humphreys, Romani, Olson, Riddoch, & Duncan, 1994; Pavlovskaya, Sagi, Soroker, & Ring, 1997) or connectedness across the vertical midline (Brooks, Wong, & Robertson, 2005) all aid in the recovery of contralesional information that might otherwise have been ignored.

It is also the case that the extent of the competition may be moderated by top-down factors. One such endogenous factor is the task demands: whereas neglect patients can correctly enumerate the number of items in a visual scene when instructed to do so, they are nonetheless unable to localize the stimuli when the task is to report the location of the items (Vuilleumier & Rafal, 2000). Task demands can also result in a subjective criterion shift adopted as a function of expectancies generated by the change in instructions (Duncan et al., 1999; Ptak et al., 2002). For example, when the distribution of attention in neglect was examined by manipulating the predictability of the side of the stimulus presentation using blocked rather than randomized trials, there was a speed up of response in both fields but no change in contra-ipsilesional differences (Natale, Posteraro, Prior, & Marzi, 2005; Rapsack, Watson, & Heilman, 1987; Smania et al., 1998). Similarly, Kaplan, Verfaellie, DeWitt, and Caplan (1990) reported that patients were more likely to report the left item on bilateral trials when it was preceded by several right unilateral trials compared to a single right unilateral trial, or a single left unilateral trial compared to several left unilateral trials (see also Mattingley et al., 2000). Even the magnitude of an exogenous cue validity effect can be modulated by the predictiveness of the cue in patients with neglect (Friedrich, Egly, Rafal, & Beck, 1998). The change in criterion and use of expectations in a top-down fashion are thought to activate a weakened representation of the contralesional stimulus, which, although not zero, might otherwise have lost out in a winner-take-all system (for advantages to contralesional stimuli in neglect dyslexia conferred by top-down lexical representations, see Behrmann, Moscovitch, Black, & Mozer, 1990; Kumada & Humphreys, 2001).

Recently, we have explored the extent to which the probability of target location affects the speed and accuracy of target discrimination in a visual search task. In normal individuals, spatial probability operates as an attentional cue that facilitates target detection, but also differs from both traditional explicit endogenous (such as an arrow cue) and salient exogenous cues (Geng & Behrmann, *in press*). We also showed that individuals with neglect benefit under conditions in which the target appears with greater frequency on the left side of space than when it appears with equal frequency on both sides (Geng & Behrmann, 2002). Not only was discrimination for left-sided targets facilitated in the neglect patients but the magnitude of the facilitation mirrored that of the control participants.

Although these various studies confirm the ability of the neglect patients to exploit the statistical contingencies associ-

ated with location probability, it is unclear whether this form of attentional cueing has any impact on the competition between left- and right-sided stimuli. In our previous experiment, multiple distractors appeared with the target on every trial, but the effect of competition is known to be dependent on the location of the target and distractors. For example, ipsilesional distractors have been found to impair detection of contralesional targets (and, unsurprisingly, the extent of the cost in reaction time was magnified as the number of distractors increased) whereas contralesional distractors did not impair processing of ipsilesional targets (Brooks et al., 2005; Egly, Robertson, & Knight, 1989; Geeraerts, Lafosse, Vandenbussche, & Verfaillie, 2005). Similarly, in several studies with normal individuals, it has been shown that the probabilistic bias effectively cues the target and reduces interference from distractors commensurate with the strength of the predictive cue (Hoffmann & Kunde, 1999; Miller, 1988; Patel & Sathian, 2000; Yantis & Egeth, 1999). The critical question to be addressed here, therefore, is whether the probability of target location can lead to increased activation of the contralesional target so as to modulate the competition from the ipsilesional distractors.

In this study, we compared the top-down spatial probability facilitation in patients with neglect and control participants in a paradigm in which a distractor did or did not accompany the target in the homologous location on the opposite side of space. The baseline condition measured the accuracy and speed of discriminating a target appearing alone but with equal probability in one of six possible screen locations, from the extreme left to extreme right of the display. The spatial bias was implemented by changing the probability of the target location so that the target appeared in the mid-left position on 50% of the trials and in the other five locations equally often on the remaining 50% of the trials (10% in each position). This design mirrors that of Geng and Behrmann (2002) and the expectation is that report of stimuli on the left will improve on the biased compared to the equal probability block in both the neglect and control groups. The competitive effects were explored by repeating the equal and biased block within the same individuals but now including a distractor concurrent with the target stimulus in the homologous location on the opposite side of space. The prediction was that an ipsilesional distractor would increase the amount of contralesional neglect. The central question, however, was whether the reduction in contralesional neglect associated with location probability would reduce interference from the ipsilesional distractor. If so, this would suggest that the probability of occurrence of the stimulus in a certain location plays a powerful role in the competition for attentional selection and that sensitivity to statistical contingencies may be a key element in offsetting the adverse impact of an ipsilesional bias in a winner-take-all system.

2. Methods

2.1. Participants

Five right-handed individuals (four males), diagnosed as having hemispatial neglect using standard neuropsychological neglect battery tests (Table 1)

Table 1
Patient demographics and performance on diagnostic tests

Patient	JM	JD	MB	MJ		DL
Age	53	64	59	59		59
Sex	M	M	F	M		M
Handedness	R	R	R	R		R
Field defect	No	L superior (pre-existing)	No	No		No
Infarct area	R temporal, frontal–parietal, R occipital adjacent to lateral ventricle	R temporal, parietal and frontal	R parietal	R frontal and temporal		R frontal–parietal
CT/MRI	CT	CT	CT	CT		MRI
Duration of cerebrovascular illness (months)	1	4	1	145		23
Line cancellation (L, R)	12/18, 18/18	0/18, 16/18	18/18, 18/18	15/18, 18/18	Star cancellation	24/27, 26/27
Example representational drawing/copying					Bells cancellation	0/17, 15/17
Letter cancellation (L, R)	13/20, 15/20	0/20, 4/20	3/20, 20/20	12/20, 13/20	Mesulam shape cancellation	1/30, 21/30
Line bisection (deviation for each of three lines)	NA	Skipped, .25", .6"	1.3", 3", 3.1"	-.25, -.25, -.25		(Over-compensates) -1.5", -.5", .7"
Test-experiment time interval	Same day	1 Week	Same day	4 Months		2 Months

and seven elderly control participants with no known neurological history (five females, aged 67–80 years old), recruited through the Academy for Lifelong Learning at Carnegie Mellon University, participated in this study. Participants in the neglect group were selected based on behavioral performance on neglect tests, and visual field defects were assessed clinically by confrontation. All individuals gave informed consent to participate in the experiment and the protocol was approved by the Institutional Review Boards of Carnegie Mellon University and the University of Pittsburgh.

2.2. Design

Each trial consisted of two consecutive displays. The first display consisted of a number presented at fixation with three evenly spaced squares in each visual field. Each square contained a mask stimulus (Fig. 1). In the second display, the number and masks disappeared, revealing either the letter "F" or "C" in one of the squares. Importantly, both letters were constructed out of segments of the mask so that there was no sudden feature onset when they appeared (Yantis & Jonides, 1990). Each square spanned approximately 2.6° of visual angle, at central fixation, and the entire display spanned approximately 28.2° of visual angle. The squares, masks, and target letters were orange in color. The central number spanned approximately 1.5° of visual angle and was green. The background was black.

The experiment had a 6 (target location) × 2 (probability) × 2 (display) factorial design. The six target locations corresponded to the position of the six squares on the screen (1, 2, 3, 4, 5, 6), numbered from left to right. Note that the numbers are shown for convenience here and were not part of the display (see Fig. 1). The two probability levels referred to blocks of trials in which the target was either equally distributed across all six locations (equal probability) or biased to appear in location 2, which was in the neglected visual field for all patients (biased probability). In the biased condition, the target appeared in location 2 on 50% of the trials and in each of the other five locations on 10% of the trials. The two display levels referred to whether the target appeared alone or simultaneous with a distractor stimulus (alone, distractor). In the distractor condition, an "E" stimulus was in

the location mirroring the target in the opposite visual field (i.e., targets in the 1, 2, 3, 4, 5, 6 locations were accompanied by distractors in the 6, 5, 4, 3, 2, 1 locations, respectively). The experiment consisted of six blocks presented in the following order: equal–alone, biased–alone, equal–distractor, biased–distractor, equal–alone, equal–distractor. Equal probability blocks consisted of 60 trials and biased probability blocks consisted of 100 trials. The location of the target on any given trial was randomly determined within the constraints of the probability parameters for that block. The equal blocks were averaged together to control for practice effects across the experiment. No data for the fifth and sixth blocks were collected for JD due to time constraints.

2.3. Procedure

Each trial proceeded in the following way: the first display screen appeared and participants verbally reported the presented digit to ensure that they were centrally fixated. Immediately following verbal report of this digit, the experimenter pressed a mouse key, which initiated the second screen. The participant then had an unlimited amount of time to determine which of the two possible targets, "F" or "C", was on the screen and to make a manual response to indicate their decision. If patients were clearly distracted, the trial was advanced by the experimenter and classified as an error. For two participants, the "j" and "i" keyboard keys were used and for the remaining participants and all control participants, the left and right mouse keys were used to indicate the presence of "F" and "C", respectively. Mouse keys were generally more comfortable for participants to manipulate and were therefore less prone to response errors. All participants responded with their right hands. Participants were seated approximately 40 cm from the computer screen. The experimenter always sat to the right of the participant. Stimulus display and data collection were conducted using E-prime (Psychology Software Tools, Pittsburgh, PA) and Cogent 2000 (Wellcome Department of Imaging Neuroscience, UCL) software. Data analysis was conducted with R software (www.r-project.org). Both accuracy and RT were collected for each trial.

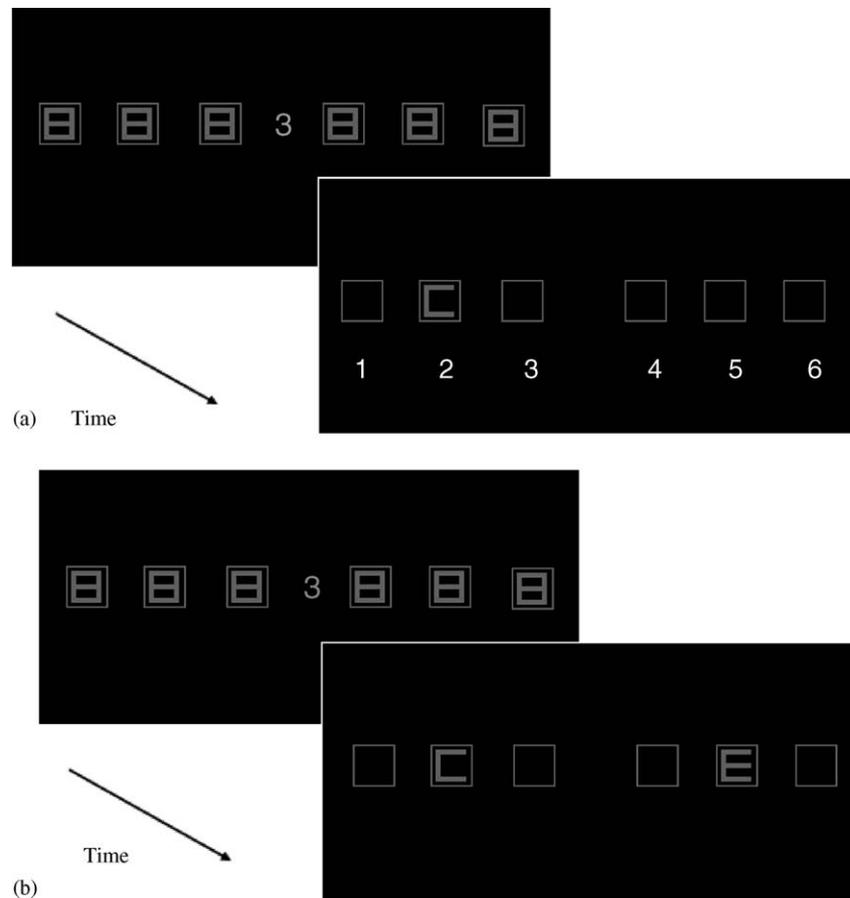


Fig. 1. Example procedure for (a) target alone and (b) target with distractor trials. Labels of the six locations 1–6 from left to right are included only for illustration. Each trial began with masks in the squares and a centrally presented number. After the participant reported the number, the masks disappeared leaving a target (and distractor) visible on the screen. The central number was green in color and the boxes, masks, and letter stimuli were all orange in color against a black background. Participants had an unlimited amount of time to make a manual response indicating which of two possible targets, C or F, was present on the screen.

3. Results

The fact that a target was present on every trial and that the choice was simply binary resulted in high accuracy (mean percent correct: patients = 98.8; controls = 99.3) and we, therefore, only report reaction time (RT) data for both patients and controls. The data were transformed using the log transform because the range of RTs both between and within the patients varied considerably. Analyses were based on the means of mean log transformed RT values for each participant in each condition, however, we additionally report mean values in absolute RT as a reference to participants' performance efficiency.

The data were entered into a repeated measures four-way ANOVA that included group (control, neglect), target locations (1, 2, 3, 4, 5, 6), probability (equal, biased), and display (alone, distractor). The full four-way interaction between group, probability, display, and target location was not significant ($F(5,50) = 1.7, p = .14$) (Fig. 2), and we report the results in four sub-sections. First, we report the basic effects of group in order to establish the expected patterns of difference between the control and neglect participants. The second and third sections report the relative effect of group and location on the probability and display manipulations, respectively. The final section

addresses the joint effects of probability and display on performance in each group (Table 2).

3.1. Group differences

There was a significant interaction between group and target location ($F(5,50) = 8.32, p < .001$): the neglect group showed the characteristic exaggerated gradient of increasing RTs with increasingly eccentric targets on the contralesional left but not on the ipsilesional right side and controls showed a symmetrical effect of target eccentricity. There was also a significant main effect of group ($F(1,10) = 6.75, p < .05$) with the patients responding significantly more slowly than controls (means in log RT and RT (ms): controls = 6.7, 886.7; patients = 7.4, 2221.8) and a significant main effect of location ($F(5,50) = 5.5, p < .0005$), reflecting the overall effect of slower responses to more eccentric targets. These results confirmed the presence of the characteristic attentional gradient associated with hemispatial neglect and the expected roughly U-shaped function for the control participants.

Note that, although the mean age of the control group is older than that of the patients, the control subjects nevertheless still perform better than the patients in all conditions. More impor-

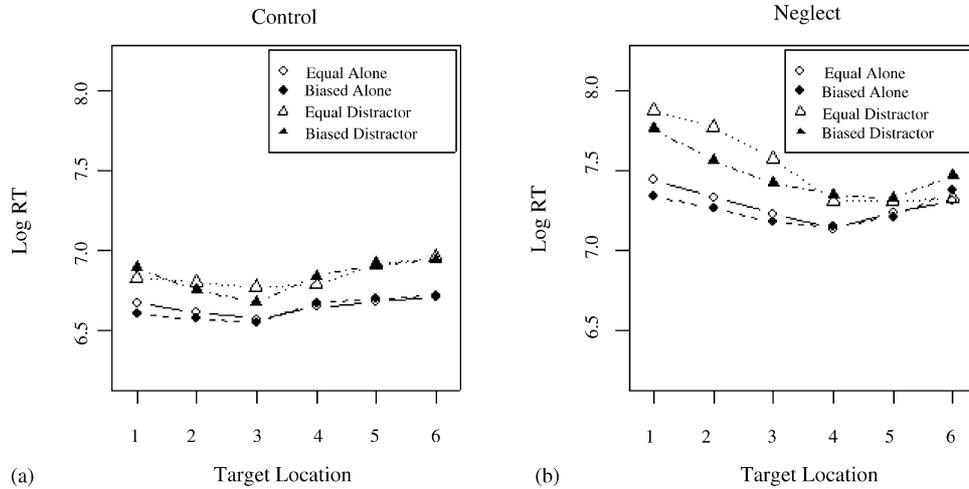


Fig. 2. Four-way interaction between group, target position, probability, and distractor competition. Although this interaction is not statistically significant, it is included for illustration of the overall pattern of data in each group.

tantly, it is the within-group comparisons of the effects of the varying attentional manipulations that are the primary focus of the study and the next sections explore these patterns.

3.2. Spatial specificity of location probability

There was no main effect of probability ($F(1,1) = 2.6, p > .1$), and no significant interaction between probability and group ($F(1,10) = .9$). The three-way interaction between group (control, neglect), target location (1–6), and probability (equal, biased) was significant ($F(5,50) = 3.85, p < .001$) and reflected a stronger and more distributed probability bias in the neglect than control group (Fig. 3a). Note that these data collapsed across the factor of display and therefore included the data from both the target alone and distractor trials.

In order to examine the effect more carefully, we calculated the normalized difference scores between RTs in the equal and biased conditions for each location ((equal log RT – biased log RT)/(equal log RT + biased log RT)) (Fig. 3b). Positive scores indicated relative facilitation for targets in the biased compared to equal condition whereas negative scores suggested relative inhibition. The normalized difference scores for each participant were entered into a 2×6 ANOVA with the factors

group (control, neglect) and target location (1–6). Consistent with the previous result, there was a significant interaction ($F(5,50) = 3.50, p < .01$). Paired t -tests revealed that the source of the interaction was predominantly in the differences at locations 1 and 6 ($t(10) = 5.9, p < .05$ and $t(10) = 4.6, p = .05$, respectively) (Fig. 3b). The difference scores at these two locations were near zero for the control group indicating there was no effect of the probability bias at the extremes. For the neglect group, however, there was positive facilitation at location 1 and negative slowing at location 6. That is, in the neglect group, RTs were faster for far-left targets in the biased compared to the equal condition, but slower for far-right targets in the same comparison.

There was also a trend, but no significant difference at location 2 between groups, both of which showed faster performance in the biased than the equal condition ($t(10) = 2.8$), and no group differences in location 3, again with both groups showing facilitated target discrimination in the biased condition. Note that because the dependent measure is normalized, the relative differences between the groups cannot be attributed simply to the increased opportunity for facilitation or inhibition in the neglect group because RTs were slower overall. Instead, any group differences reveal reliably different patterns between the neglect and control individuals (Table 3).

Table 2
RT in milliseconds

	Control group				Neglect group			
	Equal		Biased		Equal		Biased	
	Alone	Distractor	Alone	Distractor	Alone	Distractor	Alone	Distractor
1	798.6	744.4	946.7	1007.2	2106.1	1808.8	4325.0	3411.5
2	756.7	724.5	929.7	867.3	1921.2	1614.0	3809.3	2848.4
3	726.0	702.9	896.6	807.1	1615.8	1451.4	2726.8	2307.8
4	782.2	801.9	902.4	949.5	1556.7	1475.0	2044.9	2272.1
5	803.1	815.9	1021.4	1020.5	1718.7	1603.7	2031.1	2124.1
6	830.5	839.8	1079.5	1046.6	1922.6	1957.4	1970.2	2700.3

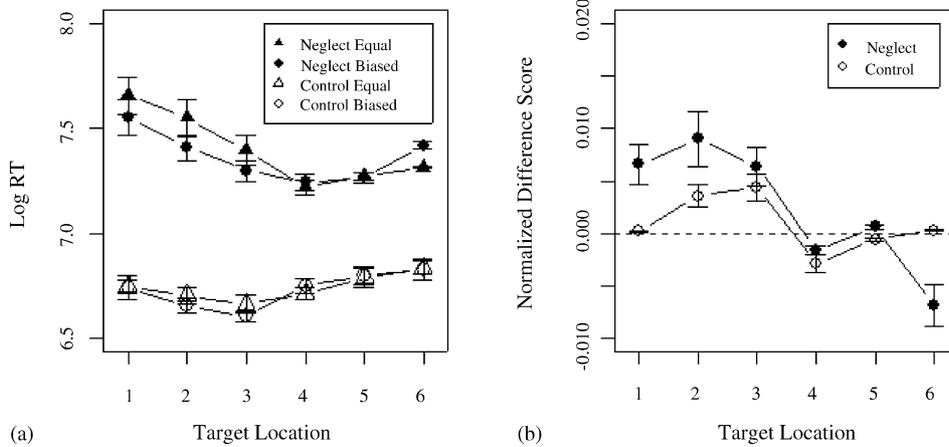


Fig. 3. (a) Three-way interaction between group, target location, and probability, showing a larger and more distributed effect of location probability in the neglect group than the control group. (b) Normalized log RT difference scores for biased compared to equal probability targets in each population group for each location. Difference scores were calculated as ((equal – biased)/(equal + biased)). The line through zero represents no difference in RT between the biased and equal conditions in that location. Positive scores indicate facilitation and negative scores indicate relative inhibition for targets in the biased compared to the equal condition.

Table 3
RT in milliseconds

	Control group		Neglect group	
	Equal	Biased	Equal	Biased
1	872.6	875.8	3215.6	2610.1
2	843.2	795.9	2865.3	2231.2
3	811.3	755.0	2171.3	1879.6
4	842.3	875.7	1800.8	1873.5
5	912.2	918.2	1874.9	1863.9
6	955.0	943.2	1946.4	2328.9

3.3. Effect of competition

We now examine the extent to which the presence of a distractor in the display impacts target discrimination on the left versus the right side. There was a significant main effect of display ($F(1,10) = 14.22, p < .01$) such that RTs were slower overall when a distractor was present than absent (means

in log RT and RT (ms): target alone = 6.9, 1253.2; with distractor = 7.1, 1835.2). The presence/absence of the distractor did not interact with group ($F(1,10) = .11$). However, the three-way interaction between group (control, neglect), target location (1–6), and display (alone, distractor) was significant ($F(5,50) = 10.02, p < .001$) (Fig. 4a). These data collapsed across equal and biased probability blocks. In order to simplify the interaction, we again calculated normalized difference scores ((target alone log RT – distractor log RT)/(target alone log RT + distractor log RT)), for each target location for each participant. A score of zero meant no difference between RTs to targets with distractors and targets alone. Increasingly positive scores represented an increasing degree of distractor interference on target processing.

The normalized difference scores were entered into a 2×6 ANOVA with the factors group (control, neglect) and target location (1, 2, 3, 4, 5, 6). The interaction was significant, $F(5,50) = 9.3, p < .001$ (Fig. 4b). The control group showed a roughly symmetrical “U” pattern in which the difference scores

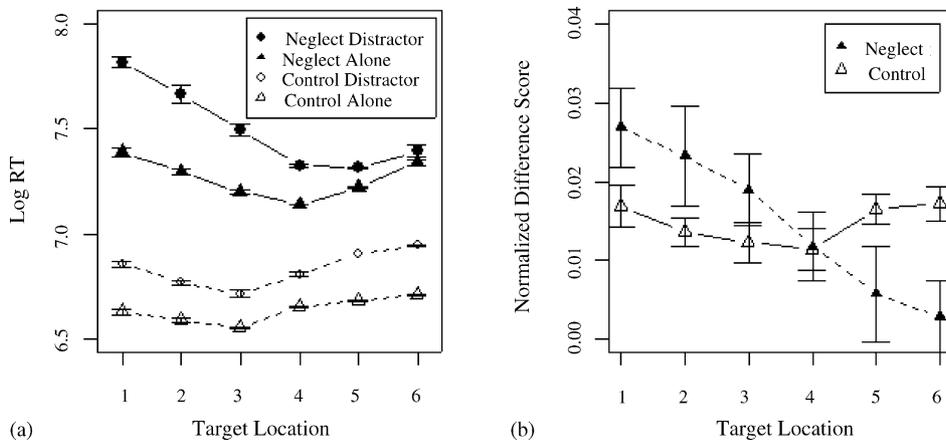


Fig. 4. (a) Three-way interaction between group, target location, and display showing a symmetrical effect of target eccentricity and distractor interference in the control group and an asymmetrical pattern in the neglect group. (b) Normalized log RT difference scores for distractor compared to target alone trials in each group and target location ((distractor – alone)/(distractor + alone)). Zero scores represent no added interference in the presence of a distractor. Positive scores indicate the degree of interference evoked by the presence of a distractor compared to a target alone trial.

Table 4
RT in milliseconds

	Control group		Neglect group	
	Alone	Distractor	Alone	Distractor
1	771.5	977.0	1957.5	3868.2
2	740.6	898.5	1767.6	3328.8
3	714.4	851.8	1533.6	2517.3
4	792.0	925.9	1515.9	2158.5
5	809.5	1020.9	1661.2	2077.6
6	835.2	1063.1	1940.0	2335.3

Table 5
Log RT and RT in milliseconds for targets in position 2

	Control group		Neglect group	
	Alone	Distractor	Alone	Distractor
Random	6.61, 756.7	6.79, 929.7	7.33, 1921.2	7.77, 3809.3
Biased	6.56, 724.5	6.74, 867.3	7.26, 1614.0	7.55, 2848.4

were greater for the most eccentric compared to the most central targets on both the left and right (location 1 versus 3: $t(6) = 3.0$, $p < .05$; location 4 versus 6: $t(6) = 3.9$, $p < .01$). Importantly, the pattern of increasing distractor interference at more eccentric locations was symmetrical on both sides. In contrast, the pattern was asymmetrical in the neglect group and showed a linear decrease from left to right. Performance on left-sided targets was similar to the control group in that there was more interference with more eccentric target–distractor pairs, but for right-sided targets, the opposite was true: more central left-sided distractors interfered more with processing of right-sided targets. In fact, the normalized difference score for location 6 was .002, a near zero difference in RT for targets with distractors and targets alone. In contrast, the difference score for location 4 was .012, suggesting greater distractor interference (the difference between these two was marginally significant, $t(4) = 2.5$, $p = .07$). These results suggest that right-sided stimuli tend to win the competition for attention, regardless of whether it was a target or distractor, but that contralesional distractors also interfered with processing when the ipsilesional target was central and proximal to the distractor (Table 4).

3.4. Interaction between competition and probability bias

The previous analyses demonstrated that the presence of the ipsilesional bias in the neglect group exaggerated the facilitatory and inhibitory effects of the spatial bias and of the distractor, respectively. However, because our a priori question dealt with the specific effect of group, probability, and display competition, we conducted six location-specific ANOVAs with the factors group, competition, and probability. The three-way interaction was significant at location 2 and survived Bonferroni correction for multiple comparisons ($F(1,10) = 13.0$, $p < .005$). The interaction was not significant at any of the other five locations (loc 1, $F(1,10) = 2.7$; loc 3, $F(1,10) = .1$; loc 4, $F(1,10) = .01$; loc 5, $F(1,10) = .5$; loc 6, $F(1,10) = 1.0$). The effect at location 2 was driven by the fact that there was less of a cost associated with the presence of a distractor stimulus in the biased compared to the equal condition in neglect patients (Table 5). This comparison was still significant even when the difference scores were normalized to control for absolute RT magnitude ($F(1,10) = 9.44$, $p < .05$) (Fig. 5). Responses to the target were slowest in the neglect group when a distractor was present, and the facilitation afforded by the probability bias at location 2 was commensurate with the degree of competition present.

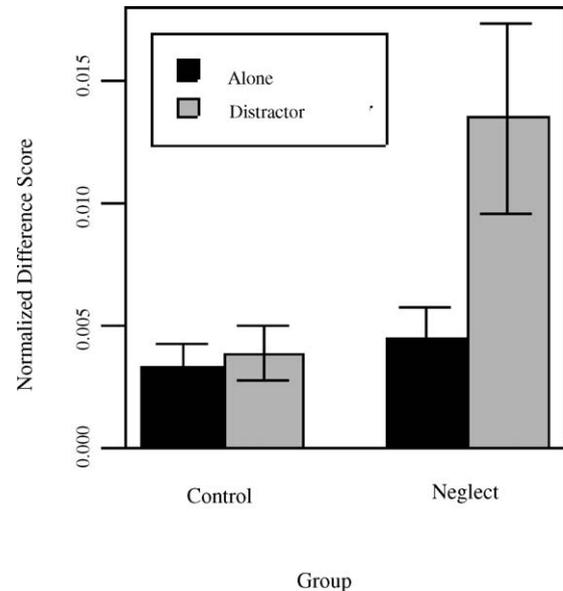


Fig. 5. Data from high probability location 2 trials showing the interaction between competition, induced by the presence of the distractor, and group using normalized difference scores from the two probability conditions. Difference scores are calculated as $((\text{equal} - \text{biased})/(\text{equal} + \text{biased}))$ using log RT.

4. Discussion

A key element of many contemporary theories of selective attention is that there are competitive interactions between concurrent stimulus events (Desimone & Duncan, 1995a; Duncan et al., 1997). Attentional studies with normal participants have suggested that the competition for selection and representation of targets from the input may be influenced by a host of factors and that the ultimate selection is the dynamic outcome of these various influences. Similar findings from single unit studies with awake, behaving monkeys indicate that competitive interactions are influenced by both bottom-up or stimulus driven factors such as the relative contrast of the stimuli in the field (Reynolds & Desimone, 2003) and by top-down feedback factors such as the task or behavioral relevance of one stimulus over another (Luck, Girelli, McDermott, & Ford, 1997). In light of these theoretical developments, hemispatial neglect has increasingly been interpreted within this same competition framework: the central idea is that, following hemispheric damage, ipsilesional information is biased along an attentional gradient with the result that the more ipsilesional of two inputs will emerge as the victor of the competition.

The primary purpose of the current study was to explore how location probability modulates this attentional competi-

tion between simultaneously-presented stimuli in patients with neglect. Our basic results demonstrated that the attentional factors we examined, spatial probability, distractor competition, and even the tonic ipsilesional bias in hemispatial neglect, all contribute and interact to bias attentional selection of information across visual space. While the strength of these biases is often unequal (some of which are determined by experimental manipulation as in the probability-biased trials), the outcome demonstrates the dynamic nature of attentional processes in determining perceptual outcomes.

4.1. *Effect of location probability on neglect*

Prior to examination of the interaction of factors, we first needed to establish the independent effects of our manipulation of probability and of distractor presence on the fundamental competition between left and right sensory inputs. The probability manipulation involved changes in the likelihood of the target appearing in the middle-left location from random to 50%. This change in probability resulted in facilitated responses to targets in that position as well as the adjacent central-left position in both the control and neglect groups. This demonstrated that the probability manipulation was effective in biasing the competition in both groups towards the most likely location. Because the stimuli were always arranged in a horizontal row, the fact that the more central location was also facilitated was not surprising and suggested that the location bias “drew” attention towards that location from the ipsilesional right, allowing faster detection of intermediate targets as well. More surprising, however, was the trade-off between the extreme left and right positions in the neglect group. The far-left location was facilitated and the far-right location inhibited, demonstrating an exchange in competitive strength between attention to these extreme locations within the context of an existing ipsilesional bias in neglect patients. In contrast, these locations were not affected by the spatial bias in the control group suggesting that spatial probability influences can be relatively specific within an intact spatial system. That the neglect patients can benefit from the probability manipulation replicates our previous results as well as other studies supporting top-down modulation of neglect (Geng & Behrmann, 2002; Natale et al., 2005; Ptak et al., 2002; Smania et al., 1998).

Although the neglect patients can exploit the statistical contingencies, they do so in a rather imprecise way. There are several possible explanations for this spatial imprecision. For example, it may be that, in neglect patients, contralesional space is either expanded or compressed (Bisiach, 1996; Halligan & Marshall, 1991) and that stimuli are not well localized spatially (di Pellegrino & de Renzi, 1995; Shalev & Humphreys, 2000). Such spatial distortions may prevent the formation of an accurate representation of any single location on that side of space. If there is no precise mapping between external location in space and an internal representation, any bias that alters the strength of the internal representation of a particular location will be only loosely mapped onto currently visible stimuli. Another possibility is that spatial precision is lost during eye-movements to and away from the target. Even in normal participants, it has been

shown that space is compressed during the period immediately preceding a saccade (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Ross, Morrone, & Burr, 1997) and that representations of spatial locations are remapped between parietal cortical hemispheres in order to update visual spatial information (Merriam, Genovese, & Colby, 2003). If the remapping of spatial locations that produces an accurate spatial representation is lost during acquisition of the target and return to fixation (Pisella & Mattingley, 2004), then the representation of the bias would be similarly imprecise.

The results from this experiment do not differentiate between possible mechanisms underlying the imprecise spatial bias in neglect but demonstrate that the likelihood of the target appearing within a single location operates on a relatively spatially specific representation in the control group and at least at the level of hemifield competition in the neglect group. In the neglect group, the probability bias shifted attention towards the contralesional side, which effectively shifted attention away from the opposite side. This finding underscores the point that the ipsilesional bias in neglect involves a biased competition of attention across space, which, despite appearing overwhelmingly strong, is still susceptible to modulation by competition from other external sources. Interestingly, none of the patients reported or demonstrated any explicit knowledge of the uneven distribution of targets, as was also the case in our previous study (Geng & Behrmann, 2002). This is consistent with the finding that neglect patients are able to direct their attention to the contralesional side (Riddoch & Humphreys, 1983), but do not overtly orient leftwards, left to their own devices. This suggests that the probability bias did not operate as an explicit attentional cue, but rather implicitly increased attentional orientation towards the most likely location.

4.2. *Impact of probability manipulation on ipsilesional competition*

The probability manipulation had a clear effect of facilitating target detection on the contralesional side. The susceptibility of the neglect bias to competitive effects from other attentional biases was also demonstrated in the opposite fashion with distractor competition. Unsurprisingly, distractors interfered with target processing in both the control and neglect groups. In control participants, responses were slower with more eccentric target–distractor pairs, but to an equal extent on both sides of space. In the neglect group, however, distractor competition exacerbated the pattern of neglect on the contralesional side such that there was linear slowing with more eccentric targets. Interestingly, contralesional distractors also interfered with ipsilesional target processing, but with the opposite pattern: there was greater interference with more central locations than more eccentric ones. That is, even ‘neglected’ distractors competed with ipsilesional targets when they were close to central fixation and the target stimulus. Neglect patients clearly have a bias to attend to ipsilesional information, but the bias is not immune to the competitive properties of information in the contralesional field, although it seems to be weakened.

The push–pull competition between attentional biases was even more distinctive in the interaction between the probabil-

ity bias and distractor presence at the high probability location (location 2). Increasing attentional competition through the presence of a distractor increased the degree to which the spatial bias facilitated processing in the neglect group (or provided more opportunity for the facilitating spatial bias to be manifested). The greater was the interference, the greater were the counteracting facilitatory effects. This push–pull quality between multiple spatial biases appeared to reflect the role of attention in resolving competition by weighting the biases dynamically (Pinsk, Doniger, & Kastner, 2004). Taken together with the findings that bottom-up perceptual factors such as stimulus similarity and top-down factors such as response criterion can modulate contralateral neglect, our findings suggest that the competition is influenced by a host of constraints and that the ultimate victor of the winner-take all likely occurs via a constraint-satisfaction process into which all these factors play.

4.3. Neglect as characterized in competitive accounts

This winner-take-all idea within a competitive system has not only gained popularity in recent empirical studies but has also been shown to be tractable through various computational implementations. In one of the earlier, successful implementations of this competitive account, Cohen, Romero, Servan-Schreiber, and Farah (1994) showed how competition between two stimuli can be captured by imposing a spatial imbalance on a model that performs a simple cued reaction time task. The model produced faster reaction times to cued targets and showed the typical cost associated with invalidly cued targets, as observed in cued covert attention paradigms (Posner, Cohen, & Rafal, 1982). The crucial result, however, was that when one set of attention units was damaged, as a proxy for the right hemisphere lesion, the model was disproportionately impaired (slowed in settling to a stable state) when cued to the right and the target appeared on the contralesional left, reflecting the competition for selection between the sensory signals. Although this model was not directly conceptualized within the biased competition framework, its operation and function under damage captures the essential properties of this dynamic attention approach. A more recent implementation that is directed at the biased competition idea (Deco & Zihl, 2004) and based on similar ideas but perhaps more neurally faithful can also account for the spatial cueing effect in neglect as well as the extinction pattern of deficit.

Importantly, the models and the biased competition framework in general reflect normal attentional function and the same principles of attentional competition operate in the normal and in the brain-damaged individuals, just with a pathological spatial bias in the latter case (Mattingley, 2002). For example, in normal individuals, performance in divided attention conditions is impaired, when a second target appears simultaneously with the first target, and visual discrimination is impaired when multiple stimuli are present compared with when half the stimuli appear in advance of the second half (see Mattingley, 2002, for many examples of such studies). It is also the case that just as perceptual load can influence the outcome of the attentional competition, so can perceptual load influence the performance in hemispatial neglect. Lavie and Robertson (2001) showed

that when patients with neglect searched for a target presented foveally under low load (accompanied by a blob) or high load (accompanied by a nontarget letter), performance differed. Specifically, the hyperactivation associated with ipsilesional distractors was reduced under high load and their contribution to the competition minimized (Lavie & Robertson, 2001). Further parallels are observed from recent studies using transcranial magnetic stimulation in which rTMS to parietal cortex impedes detection of contralesional stimuli but also gives rise to significantly better than normal performance for ipsilesional stimuli (Hilgetag, Thäeoret, & Pascual-Leone, 2001) especially on bilateral displays (Mattingley, Chambers, Janko, & Stokes, 2005).

Finally, neglect patients are able to exploit probabilistic target location information, as is the case with normal individuals: the distribution of attention was sensitive to the statistics, and responses to predictable targets and distractors were faster or more accurate than responses to unpredictable ones in neglect as in the controls (Chun & Jiang, 1998; Geng & Behrmann, *in press*; Hoffmann & Kunde, 1999; Kingstone & Klein, 1991; Miller, 1988; Ptak et al., 2002; Reder, Weber, Shang, & Vanyukov, 2003; Yantis & Jonides, 1990). Regularities are of particular interest as an attentional cue for patients with neglect because awareness of the stimulus contingencies is not necessary for facilitation to occur, and this mirrors the anosagnosia that often accompanies neglect. That attentional selection in normal individuals and in patients with neglect are influenced by similar factors further attests to the generality of the biased competition account.

4.4. Conclusion

In summary, these results demonstrated that distractor interference and implicit spatial probabilities operated as influences that either exacerbated or counteracted the existing bias to orient towards the ipsilesional visual field in neglect patients and that competition for selection is determined ultimately by the combination of influences from these two sources. The results suggest that the strength of each of the two sources was a function of the necessity for selection: facilitation due to the spatial probability was greater when additional competition was present, either in the form of experimentally manipulated distractors or an existing ipsilesional bias in neglect patients. Attentive processing was therefore the outcome of dynamic competition between external distractor presence, the internal representation of target spatial likelihoods, and the pre-existing pattern of interhemispheric rivalry in healthy and damaged brains.

Acknowledgements

This research was supported by a USA Royal Society International Postdoctoral Fellowship and a grant from the Center for the Neural Basis of Cognition Pittsburgh to JJG and by a grant from the National Institutes of Mental Health (MH54246) to MB. The authors thank Margarita Sarri, Sarah Shomstein, and Grace Lee Leonard for their assistance in recruiting and testing patients, and the participants of the Academy of Lifelong Learning at Carnegie Mellon University for their participation as control subjects.

References

- Baylis, G., Driver, J., & Rafal, R. D. (1993). Visual extinction and stimulus repetition. *Journal of Cognitive Neuroscience*, 5(4), 453–466.
- Behrmann, M., Moscovitch, M., Black, S. E., & Mozer, M. (1990). Perceptual and conceptual factors in neglect dyslexia: Two contrasting case studies. *Brain*, 113(4), 1163–1183.
- Bender, M. B. (1952). *Disorders in perception*. Springfield, IL: Charles C. Thomas.
- Bisiach, E. (1996). Unilateral neglect and the structure of space representation. *Current Directions in Psychological Science*, 5(2), 62–65.
- Brooks, J., Wong, Y., & Robertson, L. (2005). Crossing the midline: Reducing attentional deficits via interhemispheric interactions. *Neuropsychologia*, 43(4), 572–582.
- Cai, R., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature*, 10(386), 601–604.
- Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology*, 36(1), 28–71.
- Cohen, J., Romero, R., Servan-Schreiber, D., & Farah, M. J. (1994). Mechanisms of spatial attention: The relation of macrostructure to microstructure in parietal neglect. *Journal of Cognitive Neuroscience*, 6(4), 377–387.
- Critchley, M. (1953). *The parietal lobes*. London: Hafner Press.
- Danckert, J., Maruff, P., Kinsella, G., de Graaff, S., & Currie, J. (1999). Attentional modulation of implicit processing of information in spatial neglect. *Neuroreport*, 10(5), 1077–1083.
- Deco, G., & Zihl, J. (2004). A biased competition based neurodynamical model of visual neglect. *Medical Engineering and Physics*, 26(9), 733–743.
- Desimone, R. (1999). Visual attention mediated by biased competition in extrastriate visual cortex. In G. W. Humphreys, J. Duncan, & A. Treisman (Eds.), *Attention, action and space* (pp. 13–30). Oxford, UK: Oxford University Press.
- Desimone, R., & Duncan, J. (1995a). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–197.
- Desimone, R., & Duncan, J. (1995b). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- di Pellegrino, G., & de Renzi, E. (1995). An experimental investigation on the nature of extinction. *Neuropsychologia*, 33(2), 153–170.
- Driver, J. (1998). The neuropsychology of spatial attention. In H. Pashler (Ed.), *Attention* (pp. 297–340). East Sussex, UK: Psychology Press.
- Driver, J., Mattingley, J. B., Rorden, C., & Davis, G. (1997). Extinction as a paradigm measure of attentional bias and restricted capacity following brain injury. In P. Thier & H. O. Karnath (Eds.), *Parietal lobe contributions to orientation in 3d space* (pp. 401–429). Heidelberg: Springer.
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 113(4), 501–517.
- Duncan, J., Bundesen, C., Olson, A., Humphreys, G. W., Chavda, S., & Shibuya, H. (1999). Systematic analysis of deficits in visual attention. *Journal of Experimental Psychology: General*, 128(4), 450–478.
- Duncan, J., Humphreys, G., & Ward, R. (1997). Competitive brain activity in visual attention. *Current Opinion in Neurobiology*, 7, 255–261.
- Eglin, M., Robertson, L. C., & Knight, R. T. (1989). Visual search performance in the neglect syndrome. *Journal of Cognitive Neuroscience*, 1(4), 372–385.
- Friedrich, F. J., Egly, R., Rafal, R. D., & Beck, D. (1998). Spatial attention deficits in humans: A comparison of superior parietal and temporal-parietal junction lesions. *Neuropsychology*, 12(2), 193–207.
- Geeraerts, S., Lafosse, C., Vandenbussche, E., & Verfaillie, K. (2005). A psychophysical study of visual extinction: Ipsilesional distractor interference with contralesional orientation thresholds in visual hemineglect patients. *Neuropsychologia*, 43(4), 530–541.
- Geng, J. J., & Behrmann, M. (2002). Probability cueing of target location facilitates visual search implicitly in normal participants and patients with hemispatial neglect. *Psychological Science*, 13(6), 520–525.
- Geng, J. J., & Behrmann, M. (in press). Spatial probability as an attentional cue in visual search. *Perception and Psychophysics*.
- Gilchrist, I. D., Humphreys, G. W., & Riddoch, M. J. (1996). Grouping and extinction: Evidence for low-level modulation of visual selection. *Cognitive Neuropsychology*, 13(8), 1223–1249.
- Halligan, P. W., & Marshall, J. C. (1991). Spatial compression in visual neglect: A case study. *Cortex*, 27, 623–629.
- Hilgetag, C. C., Thäeoret, H., & Pascual-Leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced ‘virtual lesions’ of human parietal cortex. *Nature Neuroscience*, 4(9), 953–957.
- Hoffmann, J., & Kunde, W. (1999). Location-specific target expectancies in visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 25(4), 1127–1141.
- Humphreys, G. W., Romani, C., Olson, A., Riddoch, M. J., & Duncan, J. (1994). Non-spatial extinction following lesions of the parietal lobe in humans. *Nature*, 372, 357–359.
- Kaplan, R. F., Verfaellie, M., DeWitt, L. D., & Caplan, L. R. (1990). Effects of changes in stimulus contingency on visual extinction. *Neurology*, 40(8), 1299–1301.
- Karnath, O. H. (1988). Deficits of attention in acute and recovered hemineglect. *Neuropsychologia*, 26(1), 27–43.
- Kingstone, A., & Klein, R. (1991). Combining shape and position expectancies: Hierarchical processing and selective inhibition. *Journal of Experimental Psychology: Human Perception and Performance*, 17(2), 512–519.
- Kinsbourne, M. (1993). Orientational bias model of unilateral neglect: Evidence from attentional gradients within hemispace. In I. H. Robertson & J. C. Marshall (Eds.), *Unilateral neglect: Clinical and experimental studies* (pp. 63–86). Hove, UK: Lawrence Erlbaum.
- Kumada, T., & Humphreys, G. W. (2001). Lexical recovery from extinction: Interactions between visual form and stored knowledge modulate visual selection. *Cognitive Neuropsychology*, 18(5), 465–478.
- Lavie, N., & Robertson, I. H. (2001). The role of perceptual load in neglect: Rejection of ipsilesional distractors is facilitated with higher central load. *Journal of Cognitive Neuroscience*, 13(7), 867–876.
- Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, 33, 64–87.
- Mattingley, J., Pisella, L., Rossetti, Y., Rode, G., Tiliket, C., Boisson, D., et al. (2000). Visual extinction in oculocentric coordinates: A selective bias in dividing attention between hemifields. *Neurocase*, 6(6), 465–474.
- Mattingley, J. B. (2002). Spatial extinction and its relation to mechanisms of normal attention. In H. O. Karnath, A. D. Milner, & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 289–309). Oxford, UK: Oxford University Press.
- Mattingley, J. B., Chambers, C. B., Janko, N. E., & Stokes, M. G. (2005). Parietal mediation of attentional selection in competitive visual displays. In *Paper presented at the Cognitive Neuroscience Society, New York*.
- Merriam, E. P., Genovesi, C. R., & Colby, C. L. (2003). Spatial updating in human parietal cortex. *Neuron*, 39(2), 361–373.
- Miller, J. (1988). Components of the location probability effect in visual search tasks. *Journal of Experimental Psychology: Human Perception and Performance*, 14(3), 453–457.
- Natale, E., Posteraro, L., Prior, M., & Marzi, C. (2005). What kind of visual spatial attention is impaired in neglect? *Neuropsychologia*, 43, 1072–1085.
- Patel, G. A., & Sathian, K. (2000). Visual search: Bottom-up or top-down? *Frontiers in Bioscience*, 5, D169–D193.
- Pavlovskaya, M., Sagi, D., Soroker, N., & Ring, H. (1997). Visual extinction and cortical connectivity in human vision. *Cognitive Brain Research*, 6, 159–162.
- Pinsk, M. A., Doniger, G., & Kastner, S. (2004). Push–pull mechanism of selective attention in human extrastriate cortex. *Journal of Neurophysiology*, 92, 622–629.
- Pisella, L., & Mattingley, J. B. (2004). The contribution of spatial remapping impairments to unilateral visual neglect. *Neuroscience Biobehavioral Reviews*, 28(2), 181–200.

- Posner, M. I., Cohen, Y., & Rafal, R. D. (1982). Neural systems control of spatial orienting. *Proceedings of the Royal Society of London, Series B*, 298, 187–198.
- Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of visual attention. *Journal of Neuroscience*, 4, 1863–1874.
- Ptak, R., Valenza, N., & Schnider, A. (2002). Expectation-based attentional modulation of visual extinction in spatial neglect. *Neuropsychologia*, 40, 2199–2205.
- Rapsack, S. Z., Watson, R. T., & Heilman, K. M. (1987). Hemispace-visual field interactions in visual extinction. *Journal of Neurology, Neurosurgery and Psychiatry*, 50, 1117–1124.
- Reder, L. M., Weber, K., Shang, Y., & Vanyukov, P. (2003). The adaptive character of the attentional system: Statistical sensitivity in a target localization task. *Journal of Experimental Psychology: Human Perception and Performance*, 29(3), 631–649.
- Reynolds, J. H., & Desimone, R. (2003). Interacting roles of attention and visual salience in v4. *Neuron*, 37(5), 853–863.
- Riddoch, M. J., & Humphreys, G. W. (1983). The effect of cueing on unilateral neglect. *Neuropsychologia*, 21, 589–599.
- Ross, J., Morrone, M., & Burr, D. (1997). Compression of visual space before saccades. *Nature*, 10(386), 598–601.
- Shalev, L., & Humphreys, G. W. (2000). Biased attentional shifts associated with unilateral left neglect. *Cognitive Neuropsychology*, 17(4), 339–364.
- Smania, N., Martini, M., Gambina, G., Tomelleri, G., Palmara, A., Natale, E., et al. (1998). The spatial distribution of visual attention in hemineglect and extinction patients. *Brain*, 121(9), 1759–1770.
- Vuilleumier, P. O., & Rafal, R. D. (2000). A systematic study of visual extinction. Between- and within-field deficits of attention in hemispatial neglect. *Brain*, 123(Pt 6), 1263–1279.
- Ward, R., Goodrich, S., & Driver, J. (1994). Grouping reduces visual extinction: Neuropsychological evidence for weight-linkage in visual selection. *Visual Cognition*, 1(1), 101–129.
- Yantis, S., & Egeth, H. E. (1999). On the distinction between visual salience and stimulus-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 25(3), 661–676.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, 16(1), 121–134.